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Bite Performance of Captive Alligator Snapping Turtles (*Macrochelys temminckii*) Improves after Reintroduction

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ABSTRACT.—Alligator Snapping Turtles (*Macrochelys temminckii*) possess unique head morphology that suggests strong natural selection for bite performance, which likely influences foraging and prey selection, as well as the outcomes of intrasexual aggressive encounters, mating, and defense against predators. Therefore, bite performance has the potential to directly and indirectly impact fitness. In this study, we assessed the effects of captivity on bite force by comparing the performance of captive and reintroduced *M. temminckii*. On average, free-ranging *M. temminckii* bite with greater force than do individuals residing in captivity, and captive individuals housed under seminatural conditions in outdoor ponds outperformed those housed indoors. Further, we found that free-ranging *M. temminckii* released into different river systems performed comparably and required less provocation than captives to display gaping and biting behavior. It remains to be determined whether the observed performance differences were more strongly influenced by physiological limitations on muscle performance or by behavioral variation in motivation to bite with maximum force.

Reintroduction biology encompasses a suite of tools that are widely used for the augmentation of imperiled populations of fauna and flora. Captive propagation paired with reintroduction represents one such strategy, and often also involves head-starting animals in captivity until they achieve a size that will reduce predation risk following release (Siegel and Dodd, 2000; IUCN/SSC, 2013). Although head-starting often provides a clear benefit by reducing postrelease mortality rates, captivity may result in lasting behavioral or physiological syndromes that negatively impact animals' performance in the wild (Jule et al., 2008; Crane and Mathis, 2011). For example, a review of reintroductions of mammals found that conservation efforts using captive-reared animals were less likely to succeed than those that translocated wild-caught individuals, with anomalies in behavior being the most frequently documented obstacle to success. Common behavioral syndromes included a naivety to predators and humans, as well as stunted interactions with conspecifics (Jule et al., 2008; Berger-Tal et al., 2019). In some cases, experiments have demonstrated that behavioral syndromes can be muted and survival improved by training individuals to recognize and avoid predators (Crane and Mathis, 2011). Altered phenotypes of the muscles and skeleton are chief among physiological syndromes that can afflict postrelease survival (Waddington, 1975; Travis, 1994; Schlichting and Pigliucci, 1998; Erickson et al., 2004). Captivity-induced deleterious traits can be influenced by a variety of variables including diet, temperature regime, enclosure, opportunities for social interactions with conspecifics, and opportunities to learn to identify and avoid potential predators (Frye, 1981; Arnold and Peterson, 1990; Donoghue and Langenberg, 1996; Lane, 1996).

A head-start program was launched in 1999 in southeastern Oklahoma to aid the recovery of Alligator Snapping Turtle (*Macrochelys temminckii*) populations that had been decimated by trapping and habitat degradation (Moore et al., 2013). The program, established at Tishomingo National Fish Hatchery (TNFH), includes brood stock maintained in large seminatural

ponds, indoor facilities where eggs are incubated and juveniles are reared, and ponds that function as soft-release enclosures for juveniles, allowing young animals to acclimate to outdoor conditions before release. Head-started *M. temminckii* have been reintroduced in Oklahoma, Illinois, Louisiana, and Tennessee, and these reintroduction sites also provide opportunities for dispersal into other states that lie within the species' historic range (Riedle et al., 2008). However, reintroduction success is dependent on the condition of the stock that is released. To understand potential long-term effects of captivity on the success of the reintroduction program, it is important to consider the impact of captivity on an animal's performance or its ability to perform ecologically relevant tasks (Arnold, 1983; Jule et al., 2008).

Bite force is commonly measured to assess performance in a variety of taxa, and when compared among relevant groups, can be used to address ecological questions (Herrel et al., 1999, 2002; Erickson et al., 2004; Vanhooydonck et al., 2005). Few species exhibit evidence of as strong selection for bite performance as *M. temminckii*; megacephaly, beak morphology, size of masseter muscles, and propensity to maintain a face-forward defensive stance when threatened all suggest that *M. temminckii* has undergone strong selective pressure for bite performance, with any reduction of skull architecture, musculature, or defensive behavior likely being deleterious to survival (Herrel et al., 2002; Pritchard, 2006).

To detect any adverse effects of captivity on bite performance in *M. temminckii*, we compared bite force among animals in captivity with free-ranging individuals that had been released from the head-start facility into rivers. We assessed several aspects of bite performance, including maximum force, repeatability of bite performance, latency to gape or bite, and aggressive displays prior to snapping. We hypothesized that 1) captive *M. temminckii* would underperform their free-ranging counterparts and 2) that captive turtles housed indoors would exhibit lower maximum bite force than turtles housed outdoors. We also hypothesized 3) that captive turtles would display greater latencies to gape, bite, or otherwise signal aggression than free-ranging turtles and 4) that proclivity to display

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aggression or bite with minimal provocation would correlate with higher bite-force measurements.

MATERIALS AND METHODS

Acquisition of Specimens.—During the summer of 2019, we measured the maximum bite force of captive *M. temminckii* at TNFH. Our indoor captive test group was housed inside in large holding tanks, while our outdoor captive test group resided in earthen ponds. To ensure that we tested a range of sizes, we selected turtles in groups of 5–15 from indoor tanks where they were segregated by year class, as well as opportunistically from four outdoor ponds where we captured individuals by hand.

In 2020, we also measured the bite performance of free-ranging *M. temminckii* that had been head-started at TNFH but were released at locations on the Caney and Verdigris Rivers in northern Oklahoma from 2008 to 2015. We trapped *M. temminckii* using hoop nets that were baited with frozen invasive carp. Traps were set in the afternoon and then checked and subsequently moved to new locations the following day (Moore et al., 2013; Anthony et al., 2015; Hollender, 2019). We housed *M. temminckii* in water-filled plastic totes that were kept in shade for the duration of testing and returned each turtle to its original location of capture within 72 h. We identified individuals in our study by their unique passive integrated transponder (PIT) tag numbers.

Equipment.—We measured bite force with a force transducer connected to a charge amplifier (type 9313AA2 transducer and type 5995 charge amplifier; Kistler, Winterthur, Switzerland). The transducer was housed between adjustable bite plates, a design modified from Pfaller et al. (2009). We matched each subject to one of three sizes of stainless-steel bite plates, with assignments to different plates determined by head length. With few exceptions, bite plates were covered with 3-mm-thick leather pads to provide friction and prevent injuries (Losos et al., 2002; Lappin and Jones, 2014). For the smallest test subjects, we padded the bite plates with layers of painter's tape because leather was too thick to accommodate their small gapes. We calibrated the force transducer by suspending weights from the bite plates and regressing nominal force on mass and then converting the units to Newtons. The hanging weights were positioned on the top plate at the same point at which the tip of Alligator Snapping Turtles' beaks typically made contact (Lappin and Jones, 2014). During all trials, we set the charge amplifier to a sensor sensitivity of 0.09 pC/Mechanical Unit and a range of 200 K Mechanical Units.

Morphometrics.—Prior to testing, we measured body mass, straight carapace length, head length, head width, and head height. We took all dimensional measurements parallel to the coronal and sagittal planes of the body with dial calipers or, in the case of large specimens, forestry calipers. We measured straight carapace length from the center of the nuchal scute to the pygal notch, head length from the tip of the snout to the posterior edge of the parietal scale, head width across the widest part of the skull, posterior to the orbits and anterior to the tympanum, and head height at the tallest point of the skull, which encompassed the lowest point on the mandibles and top of the parietal crest (Fig. 1).

Bite Trials.—Each performance trial consisted of three replicate measures of bite force, with 30 min rest between bites. During rest intervals, we housed turtles separately in plastic containers filled to ~20 cm with water. We recorded the quality of each bite as either “good” or “poor” based upon visual observations of

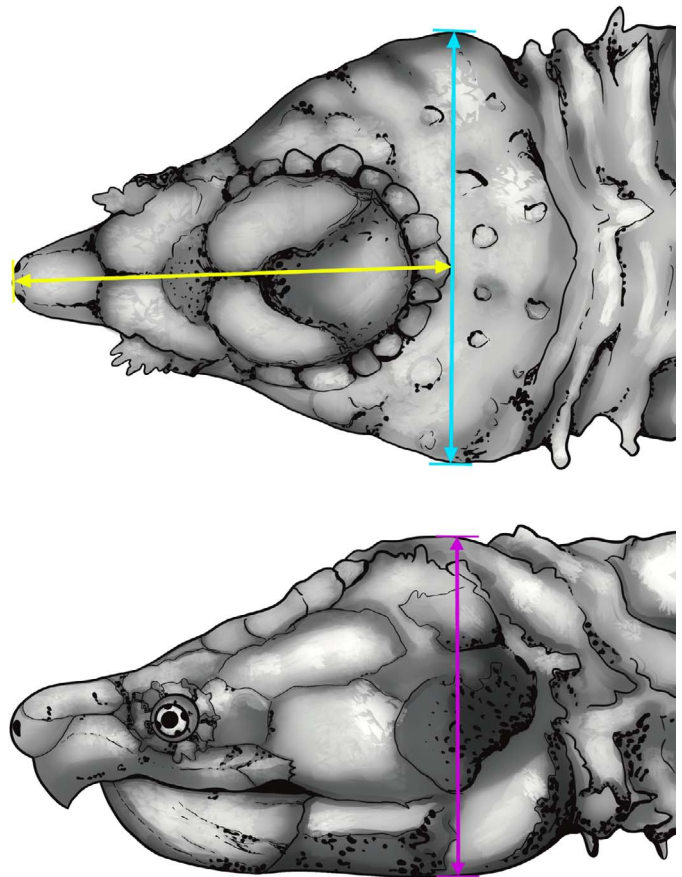


FIG. 1. Anatomical locations of head dimension measurements of *Macrochelys temminckii*, including head length (yellow), head width (teal), and head height (purple).

where the beak struck the bite plate, the angle of the head relative to the bite plate, and a qualitative assessment of the turtle's apparent motivation to bite. Bites were excluded from the data set when a turtle delivered multiple snaps on the sensor in rapid succession, and we recorded the presence of aggressive displays over the course of each bite trial including shell-raising, lunging, and snapping (Fig. 2). When presented with the bite-force apparatus, most turtles responded quickly and without additional provocation, but in cases of refusal to immediately gape or bite, we lightly tapped them on the head to elicit a defensive response and recorded latency to gape and latency to bite for each turtle as either “immediate” or “required tapping.”

To standardize data collection, we matched three sizes of stainless-steel bite plates to turtles of differing head lengths. We used small plates for turtles with head lengths 30–49 mm, medium plates for head lengths of 50–74 mm, and large plates for head lengths ≥ 75 mm. This reduced chance of injury from contact with the back of the plates and ensured that turtles interacted with a surface area of contact proportional to their head dimensions. Plates were equipped with short metal stops at their base, preventing turtles from biting too far back on the meter while also guiding the beak tips to a predictable point of contact at the back of the bite plates. Based on preliminary experiments that determined optimal test conditions, we conducted tests between 0800 and 2000 h and standardized bite plate distance at $0.25 \times$ head height (Gagnon, 2021). To target the desired ratio of head height to plate distance, we started at a head height of 30–49 mm and plate distance of 7.5



FIG. 2. A juvenile *Macrochelys temminckii* demonstrating a defensive posture that includes shell-raising and displaying a defensive gape.

mm, and moved plates apart 2.5 mm for every head height increase of 10 mm.

Data Analyses.—In assessing the repeatability of bite-force performance, we first excluded bites scored as “poor”. Prior to analysis, we $\log_{10}$ -transformed measurements of force and morphometrics to improve the distribution and homogeneity of variance among groups. We conducted analysis of covariance (ANCOVA) tests to detect differences in maximum bite force among captive and free-ranging groups. In these analyses, we included body mass as a covariate to adjust for variation in body size, and ensured that assumptions of ANCOVA were met. We selected mass over straight carapace length as a covariate in our analyses because the carapace of some individuals was damaged and therefore artificially short for their body size. However, after running the analysis against both variables, the overall trends among the data were similar. More specifically, comparisons between captive and wild turtles returned identical results, regardless of which covariate was used. We first compared maximum bite force among the two groups of captive turtles with location status (indoor versus outdoor) included as a main effect, and then compared the two groups of free-ranging turtles from the Caney and Verdigris Rivers in the same way. Upon determining differences between indoor versus outdoor captives and between free-ranging turtles inhabiting different river systems, we further analyzed differences between captive and free-ranging turtles by conducting an ANCOVA on lumped captive and lumped wild individuals. We then performed a linear regression between body size and maximum bite force by plotting maximum bite force of individuals (SigmaPlot 11.0, Systat Software, Palo Alto, California, USA). We also investigated scaling of relevant morphometrics and bite force using standard practices in scaling literature (Herrel and O’Reilly, 2005; Penning, 2017; Moon et al., 2019) using Microsoft Excel 2012 (Build 13530.20376, Microsoft).

To test the relationship between latency to gape or bite and captive versus wild status, we performed a chi-square contingency analysis using Past 4.04 with the sums of turtles from each group that required tapping versus did not require tapping when administering their strongest bite (Hammer et al., 2001). To test the relationship between latency to gape or bite and resulting maximum bite force, we performed a three-factor analysis of variance (ANOVA) with mass as a covariate, location

TABLE 1. Medians and ranges (in parentheses) of morphometric measurements and maximum bite force by group of *Macrochelys temminckii*.

Variable	Captive	Free ranging
Individuals tested (<i>n</i>)	126	61
Mass (g)	526 (60–8,150)	5375 (1,350–17,400)
Carapace length (mm)	125.2 (52.8–305.0)	278.1 (176.9–444.0)
Head length (mm)	45.3 (23.4–107.6)	92.3 (65.8–128.2)
Head width (mm)	38.8 (20.2–102.8)	89.5 (59.6–128.6)
Head height (mm)	31.1 (15.2–80.2)	68.0 (44.4–95.9)
Maximum bite force (N)	30.7 (5.8–334.1)	284.7 (69.4–814.5)

as a main effect, and willingness to gape or bite as a response variable. To test for differences in frequency of aggressive displays between groups of captive and wild individuals, we again conducted a chi-square contingency analysis with turtles that exhibited aggressive behavior assigned a score of 1 and all others assigned a score of 0. We then used a three-factor ANOVA to explore the relationship between aggressive display and resulting maximum bite force, again with mass as a covariate, location as a main effect, and aggression score as a response variable.

Except where indicated otherwise, analyses were performed in RStudio (Version 1.3.1093, PBC; RStudio Team 2020). We made our field data available to view on Figshare (<https://doi.org/10.6084/m9.figshare.19750636.v1>).

RESULTS

Captive vs. Free-ranging.—We measured the maximum bite force of 126 captive *M. temminckii* housed at TNFH. Of these, 82 resided indoors and 44 resided outdoors. All turtles were sexually immature and ranged from 60 to 8,150 g mass and 52 to 305 mm straight midline carapace length. Year classes of these subjects ranged between 2005 and 2017, with an average age at time of study of 4.5 ± 2.4 yr (mean $\pm$ 1 SD). We also measured the bite performance of 61 free-ranging *M. temminckii*. At the time of study, the mean amount of time spent free ranging was 8.3 ± 2.0 yr. Subjects consisted of sexually mature and immature individuals and ranged from 1,350 to 17,400 g mass and 177 to 444 mm straight midline carapace length. Year classes of these subjects ranged from 2004 to 2012, with an average age at time of study of 12.5 ± 2.0 yr. In total, we recorded 534 quality bites from 188 specimens, with bite force ranging from 5.8 to 334.1 N for captives, and 69.4 to 814.5 N for free-ranging individuals (Table 1). Overall, there was a positive relationship between size and maximum bite force; however, this relationship scaled differently among the groups tested (Table 2). Maximum bite force scaled to body mass with slopes of 0.68 for indoor captives, 0.75 for outdoor captives, and 0.81 for free-ranging individuals. Maximum bite force scaled to carapace length with slopes of 1.96 for indoor captive, 2.35 for outdoor captive, and 2.28 for free-ranging individuals. Finally, head dimensions scaled to bite force with slopes ranging from 0.65 to 0.78 for indoor captives, 2.09 to 2.35 for outdoor captives, and 2.61 to 3.03 for free-ranging individuals.

There was a significant interaction between body mass and location among indoor- and outdoor-housed captive turtles (interaction: $F_{1,122} = 8.54$, $P = 0.004$), and while body mass strongly predicted bite force, the resulting maximum bite forces of those housed outdoors were slightly more sensitive to

TABLE 2. Regressions of body mass and relevant morphometrics (independent variables) against bite force (dependent variable) for indoor captive, outdoor captive, and free-ranging *Macrochelys temminckii*. Slopes that differ significantly from expected allometric scaling relationships are bolded ($P < 0.05$ in all cases). In the comparison of bite force and mass, we expected a slope of 0.66, and for all other comparisons, we expected a slope of 2.0. All data were $\log_{10}$ -transformed prior to analysis, and confidence limits are 95%.

	R^2	Intercept	Slope	Confidence limits
Indoor captive				
Body mass	0.82	-0.35	0.68	0.61–0.75
Carapace length	0.82	-2.59	1.96	1.75–2.16
Head length	0.15	0.14	0.78	0.36–1.19
Head width	0.17	0.19	0.78	0.40–1.16
Head height	0.14	0.45	0.65	0.30–1.01
Outdoor captive				
Body mass	0.92	-0.45	0.75	0.68–0.81
Carapace length	0.94	-3.40	2.35	2.17–2.55
Head length	0.81	-2.22	2.35	1.99–2.70
Head width	0.77	-1.70	2.12	1.76–2.48
Head height	0.77	-1.45	2.09	1.74–2.45
Free ranging				
Body mass	0.75	-0.55	0.81	0.69–0.93
Carapace length	0.62	-3.13	2.28	1.82–2.74
Head length	0.72	-3.38	2.97	2.49–3.45
Head width	0.79	-3.44	3.03	2.63–3.43
Head height	0.75	-2.33	2.61	2.22–3.00

variations in body size than those housed indoors (Fig. 3A). There was no significant interaction between body mass and location among free-ranging *M. temminckii* inhabiting different river systems ($F_{1,58} = 0.74$, $P = 0.394$, Fig. 3B). Upon removal of this interaction, body mass predicted bite force ($F_{1,59} = 186.37$, $P < 0.0001$) and there was no significant effect of location ($F_{1,59} = 1.64$, $P = 0.205$). In a comparison of bite force of all captive versus all free-ranging *M. temminckii*, there was no significant interaction between body mass and location ($F_{1,184} = 0.64$, $P = 0.425$), and upon removal of the interaction term, body mass strongly predicted bite force ($F_{1,185} = 4,403.95$, $P < 0.0001$). However, free-ranging head-started *M. temminckii* bit with greater force than captive individuals at all sizes ($F_{1,185} = 33.06$, $P < 0.0001$, Fig. 3C). Untransformed bite force data regressed on body mass indicated that free-ranging *M. temminckii* bit with approximately 49.6 N more force than captives.

Latency to Bite and Behavior.—There was a significant difference in willingness to gape between captive and free-ranging turtles ($\chi^2_3 = 86.09$, $P < 0.0001$), with 86% of captive and 16% of free-ranging turtles requiring tapping to elicit a defensive gape (Fig. 4). Upon gaping, there was not a significant difference in willingness to bite between the groups ($\chi^2_3 = 3.00$, $P = 0.392$). In a comparison of latency to gape or bite and resulting maximum bite force, willingness to gape did not have a significant impact on the maximum bite force of captive and free-ranging turtles ($F_{1,180} = 2.97$, $P = 0.087$), but willingness to bite did ($F_{1,177} = 11.03$, $P < 0.001$). In a comparison of frequency of aggressive displays prior to biting between captive and free-ranging individuals, there was a significant difference in number of turtles that displayed pre-bite aggression among the four groups ($\chi^2_3 = 7.84$, $P = 0.049$). Captive turtles housed indoors had the highest tendency to display aggression prior to biting (71%), followed by turtles from the Caney River (53%), captive turtles reared outdoors (52%), and turtles from the Verdigris River (47%). Importantly, the display of pre-bite aggression was

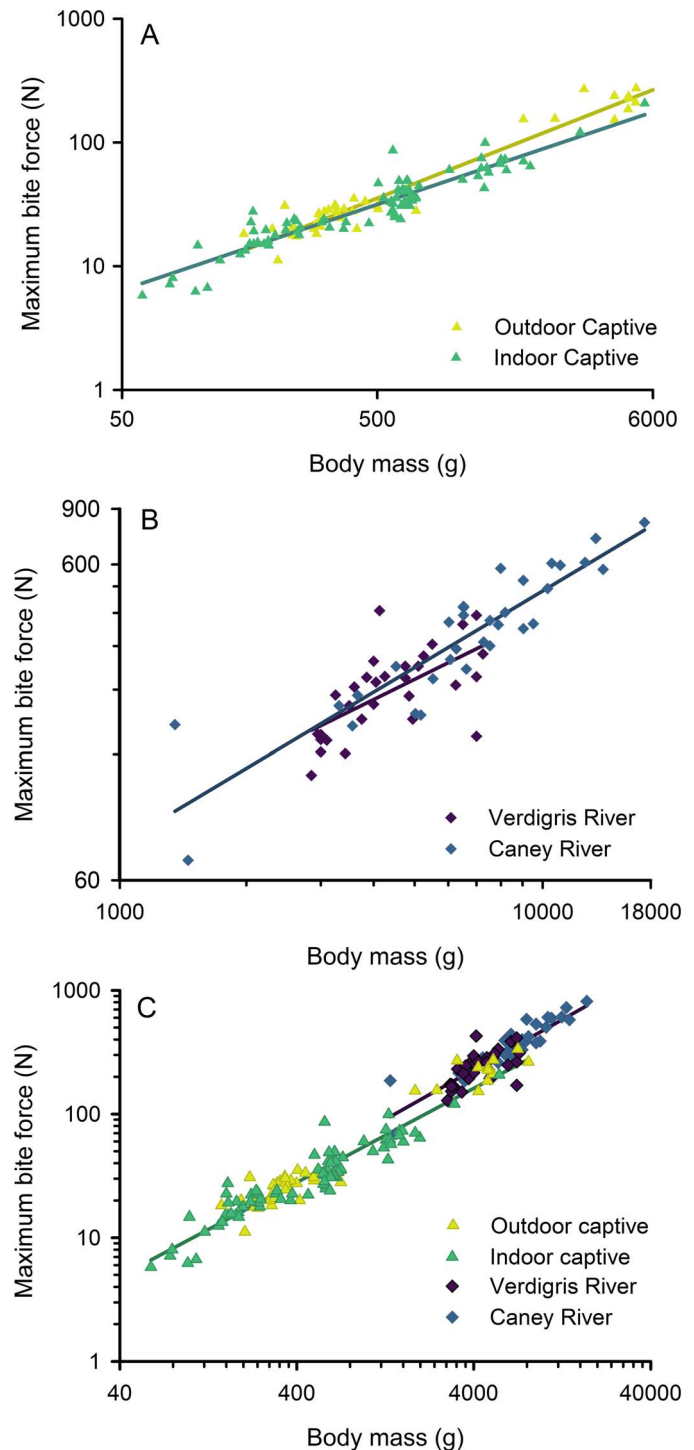


FIG. 3. Maximum bite force of (A) captive-reared *Macrochelys temminckii* housed indoors and outdoors, (B) head-started, free-ranging *Macrochelys temminckii* inhabiting the Caney and Verdigris Rivers in northern Oklahoma, and (C) lumped captive and lumped free-ranging *Macrochelys temminckii* from all locations. Note that all axes are $\log_{10}$ -transformed. Regression statistics are as follows: outdoor captive ($y = 0.81x - 0.64$, $r^2 = 0.95$, $P < 0.0001$), indoor captive ($y = 0.69x - 0.37$, $r^2 = 0.88$, $P < 0.0001$), Verdigris River ($y = 0.66x - 0.03$, $r^2 = 0.40$, $P < 0.001$), Caney River ($y = 0.80x - 0.51$, $r^2 = 0.81$, $P < 0.0001$), lumped captive ($y = 0.76x - 0.53$, $r^2 = 0.91$, $P < 0.0001$), and lumped free-ranging ($y = 0.81x - 0.55$, $r^2 = 0.75$, $P < 0.0001$).

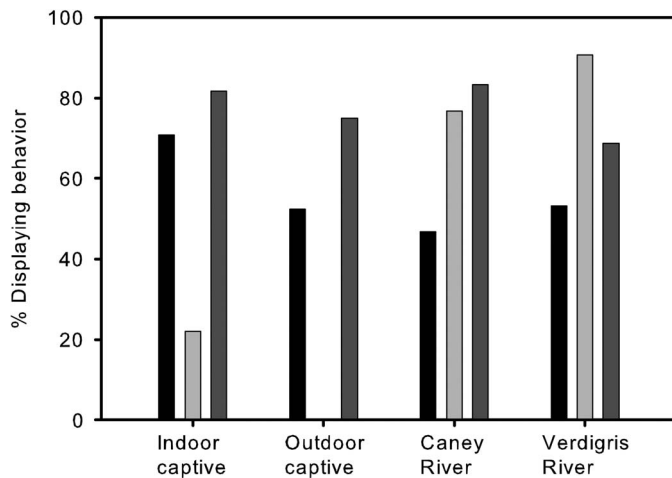


FIG. 4. Frequency of *Macrochelys temminckii* bites by group that required no provocation to elicit a gape or bite, and frequencies of pre-bite aggression displays by group including lunging, shell-raising, or snapping. Pre-bite aggression is denoted by black, immediate gape by light gray, and immediate bite by dark gray.

not a significant predictor of maximum bite force for any of the groups ($F_{1,183} = 1.31$, $P = 0.255$).

DISCUSSION

All turtles in our study originated in the same captive breeding and head-start program, yet those that had been released and were free ranging exhibited both an enhanced willingness to gape and stronger bite force than those that remained in captivity. Free-ranging *M. temminckii* exhibited greater bite forces for their size, as evidenced by elevation differences in plots of bite force relative to mass, but also followed a slightly steeper slope indicating that incremental increases in body size resulted in larger increases in bite force among free-ranging turtles. Because free-ranging turtles were larger, on average, than those in captivity, this pattern could simply reflect an ontogenetic shift in development of skull musculature, as has been observed in other species (Pfaller et al., 2011). Alternatively, it is possible that captive-born *M. temminckii* have reduced bite force in captivity and thus, upon release into natural systems, start at a performance disadvantage. Following release, environmental conditions may lead to physical challenges that were absent in captivity, causing a transition from relatively poor performers to performing at a level that would be typical of true wild specimens of comparable body size. This scenario is consistent with the fact that the captives that were maintained indoors delivered bites that scaled to head morphology at smaller-than-predicted scaling exponents, whereas those that were free ranging tended to scale to steeper-than-predicted slopes.

Among captive turtles, individuals that were housed outdoors snapped with greater force than those reared indoors under less natural conditions. Interestingly, at smaller body sizes, bite force was similar between indoor- and outdoor-housed turtles, but differences in bite performance increased at larger sizes. Therefore, bite performance is negatively impacted by prolonged captivity and the duration of a head-starting period should be balanced between achieving sizes that reduce predation and limiting deleterious effects of captivity on bite performance.

Differences in diet offer one possible explanation for reduced bite force in captive individuals when compared with that of

free-ranging turtles. Indoors, turtles primarily subsisted on a diet of fish-based food pellets which, although crunchy when dry, quickly become soft after absorbing water. Because these small pellets can generally be consumed whole, foraging likely provides little opportunity to develop strong masseter muscles that, when warranted, could produce a forceful bite. This explanation is supported by evidence that head width correlates significantly with bite force in a variety of turtle species in the wild, and that megacephaly is a phenotypically plastic trait that is sometimes enhanced in aquatic turtles when individuals forage upon hard-bodied prey (Iverson, 2020; Butterfield et al., 2021). Furthermore, differences in head size among species and between sexes of several species of turtle has been attributed to differences in diet, with groups that consume a more durophagous diet exhibiting broader heads than those that primarily target softer prey items (Lindeman, 2000, 2006).

Bite force was just one way in which defensive behavior varied among groups. Although many indoor- and outdoor-housed captives required tapping to elicit a bite, few free-ranging individuals required as much encouragement, and were more likely to skip pre-bite aggressive behaviors such as snapping, lunging, or shell-raising. Pre-bite aggressive behaviors could be tools used by less physically fit individuals to decrease chances of a physical altercation with conspecifics by looking more formidable, a phenomenon that has been observed in lizards (Lappin et al., 2006). Alternatively, it is possible these differences were influenced by a lack of predation and the increased interaction with hatchery personnel experienced by captive animals, and a subsequent reduction of defensive posture and motivation to bite (Berger-Tal et al., 2019). In comparison with those living indoors in holding tanks, captive turtles living in outdoor ponds may have benefited physically from greater space to move about, access to natural forage that likely included prey items spanning a wide range of body hardness, and fewer interactions with hatchery personnel. These factors may have increased physical fitness, reduced stress, and—with time—reduced complacency during interactions with people. In comparison with free-ranging conspecifics, on the other hand, having protection from most potential predators may have limited pond-dwelling captives' behavioral defensive response. Further, the similarity in frequency of pre-bite aggressive displays between captive turtles reared outdoors and the two populations of free-ranging turtles could suggest that time spent acclimating to the outdoors in ponds aids in preparing individuals to succeed in the wild, and contributes to efficient "post-release behavior modification," the concept that the more time a captive-reared animal spends in the wild, the better adapted it will become to its new habitat (Berger-Tal and Saltz, 2014).

Implications.—Results of previous studies of growth and survival of *M. temminckii* in the Caney River demonstrate that captive-reared *M. temminckii* thrive upon reintroduction in at least some systems (Anthony et al., 2015). However, it is critical in any reintroduction context that organisms that are released be in as near-optimal condition as possible (Berger-Tal et al., 2019). The comparatively poor bite performance of *M. temminckii* housed indoors could be used to infer that animals in these conditions should be offered a wider range of food items that vary in hardness. Alternatively, we propose that a simpler solution—and one that is already implemented at TNFH—is to minimize the amount of time housed indoors and, even more importantly, ensure that all individuals spend an extended period in outdoor ponds prior to reintroduction into natural systems. Optimizing bite performance prior to reintroduction has the potential to

expand the available prey base and reduce threats of predation, both key aspects of survival in a new environment. To further understand the roles of behavior and physiology in the bite performance of *M. temminckii*, areas of future study could include the comparison of head dimensions and muscle mass across study groups, as well as a deeper exploration of scaling relationships among morphometric and performance variables. To attain a deeper understanding of the role of head-start initiatives in turtle conservation, a future investigation of wild-hatched *M. temminckii* could provide more insight into lasting effects of captivity on bite performance.

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